

Modeling time-varying growth using a generalized von Bertalanffy model with application to bloater (*Coregonus hoyi*) growth dynamics in Lake Michigan

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Abstract: A concurrent increase in lakewide abundance and decrease in size-at-age of bloater (*Coregonus hoyi*) in Lake Michigan have suggested density-dependent growth regulation. We investigated these temporal patterns by fitting a dynamic von Bertalanffy model and length–weight relationship with time-varying parameters to mean length- and weight-at-ages (ages 1–7) from annual surveys (1965–1999). We modeled yearling length, asymptotic size (L_{∞}), and the parameters of a power relationship between mean weight and mean length (α and β) as changing slowly over time using a random walk model. The Brody growth coefficient (k) was modeled as a linear function of L_{∞} with year-specific random deviations. Our results support a positive relationship between L_{∞} and k , indicating that under conditions supporting larger asymptotic lengths, individuals approach the asymptote more rapidly. We explored the relationship between year-specific growth parameters and indices of lakewide bloater abundance and found evidence of density-dependent growth. However, in the most recent years, L_{∞} and yearling length have remained low in Lake Michigan despite low bloater abundances, suggesting the occurrence of a fundamental shift in the food web.

Résumé : Chez le cisco de fumage (*Coregonus hoyi*) du lac Michigan, la coïncidence d'une augmentation de l'abondance dans tout le lac et d'une diminution de la taille à un âge donné laisse croire à l'existence d'une régulation de la croissance dépendante de la densité. Nous avons examiné ces structures temporelles en ajustant un modèle dynamique de von Bertalanffy et des relations longueur–masse avec des paramètres qui varient dans le temps aux données de longueur moyenne et de masse à un âge donné (âges 1–7) provenant d'inventaires annuels (1965–1999). Nous avons modélisé la longueur des jeunes de 1 an, la longueur à l'asymptote (L_{∞}) et les paramètres d'une relation de puissance entre la masse moyenne et la longueur moyenne (α et β) en les faisant varier lentement dans le temps à l'aide d'un modèle de marche aléatoire. Le coefficient de croissance de Brody (k) a été modélisé comme une fonction linéaire de L_{∞} avec des déviations aléatoires spécifiques à l'année. Nos résultats indiquent une relation positive entre L_{∞} et k , ce qui veut dire que, dans des conditions qui permettent des longueurs à l'asymptote plus élevées, les individus s'approchent plus rapidement de l'asymptote. Nous avons étudié la relation entre les paramètres de croissance spécifiques à l'année et les indices d'abondance des ciscos dans l'ensemble du lac et nous avons trouvé des indications d'une croissance dépendante de la densité. Cependant, durant les dernières années, L_{∞} et la longueur des jeunes de 1 an ont été faibles au lac Michigan malgré l'abondance réduite de ciscos, ce qui laisse croire à un changement radical dans le réseau alimentaire.

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Introduction

Dynamic growth of fishes has many implications and applications in the management of fisheries, and many ecological and practical insights can be gained by examining patterns in fish growth (e.g., Ferreri and Taylor 1996; Fargo and Kronlund 2000; Walters and Wilderbuer 2000). The effects of environmental factors on growth have been examined through both ex-

perimental manipulation and observational studies. Although the experimental approach allows the strongest inferences, it is often not feasible for populations or species of interest. In many cases when an observational approach is necessary, a time series of observations of size-at-age and environmental factors are examined (e.g., Mallet et al. 1999; Millar et al. 1999; Fargo and Kronlund 2000). Because of the high variability in mean size-at-age estimates about the population's true

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mean size-at-age, it is often advantageous to identify and fit a growth model to the data to provide smoothed estimates of growth over time.

Such a model-based analysis of data from an observational study generally extends a traditional growth model, usually the von Bertalanffy model, to include time-varying parameters fit to the time series of observations (e.g., Mallet et al. 1999; Millar et al. 1999; Fargo and Kronlund 2000). The time series of observations used to fit the model is generally one of two types, size-at-age data or growth increment data calculated from size-at-age data.

Time-varying parameters have been incorporated into growth models in two general ways, through explicit functions of an environmental variable or by estimating, independently of environmental data, year-specific parameters for the growth model. Applications of the first approach (Millar and Myers 1990; Mallet et al. 1999; Millar et al. 1999) usually model either the L_{∞} or k parameter of a von Bertalanffy growth curve as function of an environmental factor, usually temperature. This approach requires identifying both the environmental factor and the functional relationship between this factor and the growth parameters. If the connection between growth and the environment is misspecified, it is possible that spurious patterns in year-specific growth could be identified.

The second approach is to fit a growth model to data on size-at-age independently for each year for which data are available (e.g., Zhao et al. 1997; Fargo and Kronlund 2000). The temporal patterns in the resulting parameter estimates can then be examined in relation to temporal patterns in factors that might cause them to vary. By independently fitting a growth model to each year of size-at-age data, however, this approach ignores the interdependence of growth between years. Here, the model is describing the pattern in size-at-age within a year, not mean growth of a given age between year y and year $y + 1$. The two are only equivalent when growth rates are not changing over time. Hence, this approach causes difficulties in interpretation.

Here we present an alternative method for applying the second approach. We use a von Bertalanffy growth curve with time-varying parameters to predict growth increments from one year to the next. We keep track of the dynamically changing predictions of size-at-age and compare these predictions with a time series of size-at-age observations to estimate the parameters of our model. Thus, the time-varying parameters are estimated independently of any proposed environmental mechanism, in contrast with the first method, and the parameters describe growth rather than year-specific patterns in size-at-age, as in many applications of the second method. Our technique uses a time series approach to model the changes in growth parameters over time and estimates these parameters using a maximum likelihood framework. We apply this approach to the growth dynamics of the bloater (*Coregonus hoyi*) population in Lake Michigan. We then explore the potential mechanisms for changes in bloater growth using the resulting growth parameter estimates.

Bloater is an important member of the Lake Michigan ecosystem. In Lake Michigan, this coregonine is the sole remaining member of an original endemic complex of deepwater forms (Todd et al. 1981). Historically, bloater populations

supported valuable commercial fisheries (Brown et al. 1987; Fleischer 1992) and were forage for the native lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) populations. Currently, they are forage for the array of stocked salmonids, especially when bloater are younger and smaller (Holey et al. 1998; Madenjian et al. 2002). Changes in bloater populations within Lake Michigan have been dramatic. Bloater abundance increased from near zero in 1970 to dominate the planktivore biomass of the lake by the late 1980s (Madenjian et al. 2002) (Fig. 1a). Bloater abundance remained high during most of the 1990s and subsequently declined to low levels again (TeWinkel et al. 2002). Concurrent with these large changes in abundance, bloater length- and weight-at-age also went through large changes (Figs. 1b–1d). These changes in size-at-age appeared to be correlated with bloater abundance, suggesting that bloaters in Lake Michigan might be exhibiting density-dependent growth (TeWinkel et al. 2002). Because bloater length- and weight-at-age have been monitored continuously since 1965 to present (except 1966 and 1998), these data provided us the opportunity to explore the changes that have occurred in the growth of bloater over time and the potential for density-dependent growth regulation in the Lake Michigan bloater population.

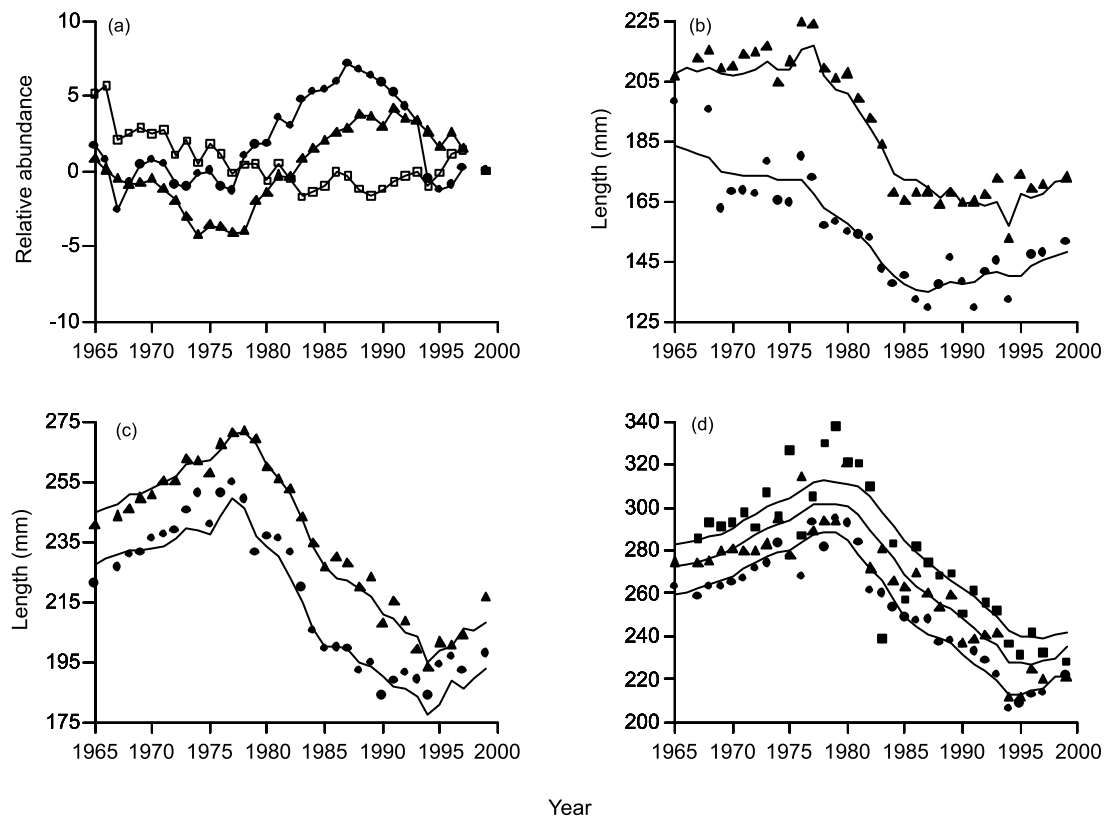
Materials and methods

The Lake Michigan bloater population has been assessed annually since 1962 by the U.S. Geological Survey (USGS) – Great Lake Science Center in a fall bottom trawl survey. This survey is conducted at fixed locations throughout Lake Michigan and provides information on the size (length and weight), age composition, and abundance (through catch-per-unit-effort (CPUE)) of the bloater population along with the exotic alewife (*Alosa pseudoharengus*) population. We used these survey data to construct a time-varying growth model for the bloater population and explored the relationship between the estimated growth parameters and abundance of both bloater and alewife.

Fall trawl survey design

To calculate mean length- and weight-at-age and abundance indices, we analyzed catch data from annual bottom trawl surveys conducted by the USGS – Great Lakes Science Center each fall (e.g., Hatch et al. 1981). The survey was initiated in 1962, but bloater were first aged in 1965 and hence we restricted our analysis to the 1965–1999 period. Trawls were generally 10 min in length and used a $\frac{3}{4}$ Yankee Standard No. 35 bottom trawl (12 m headrope, 15.5 m footrope, and 13-mm mesh in the cod end) dragged on contour during the day as described by Hatch et al. (1981). Sampling was done offshore of fixed shore locations (Fig. 2). Generally tows were made at each location at 9-m depth intervals and the sampled depths ranged from 6 to 128 m. Not all locations were sampled in each year, usually related to weather conditions, nor were all depths sampled at each location because of irregular bottom features. Although the locations were fixed, the number and identity of sampled locations did change over time. Initially, from 1962 to 1966, trawls were made only off Saugatuck, Mich. (Fig. 2), and in

Fig. 1. (a) Relative abundance of yearling bloater (*Coregonus hoyi*) (solid circles), adult (age 2+) bloater (solid triangles), and adult alewife (*Alosa pseudoharengus*) (open squares) in Lake Michigan from 1965 to 1999. Observed (symbols) and predicted (lines) mean length-at-age for (b) age 1 (solid circles, lower line) and age 2 (solid triangles, upper line), (c) age 3 (solid circles, lower line) and age 4 (solid triangles, upper line), and (d) age 5 (solid circles, lower line), age 6 (solid triangles, middle line), and age 7 (solid squares, upper line) over time in Lake Michigan.



1967, three additional locations were included. Starting in 1973, an additional three locations were added for a total of seven fixed shore locations.

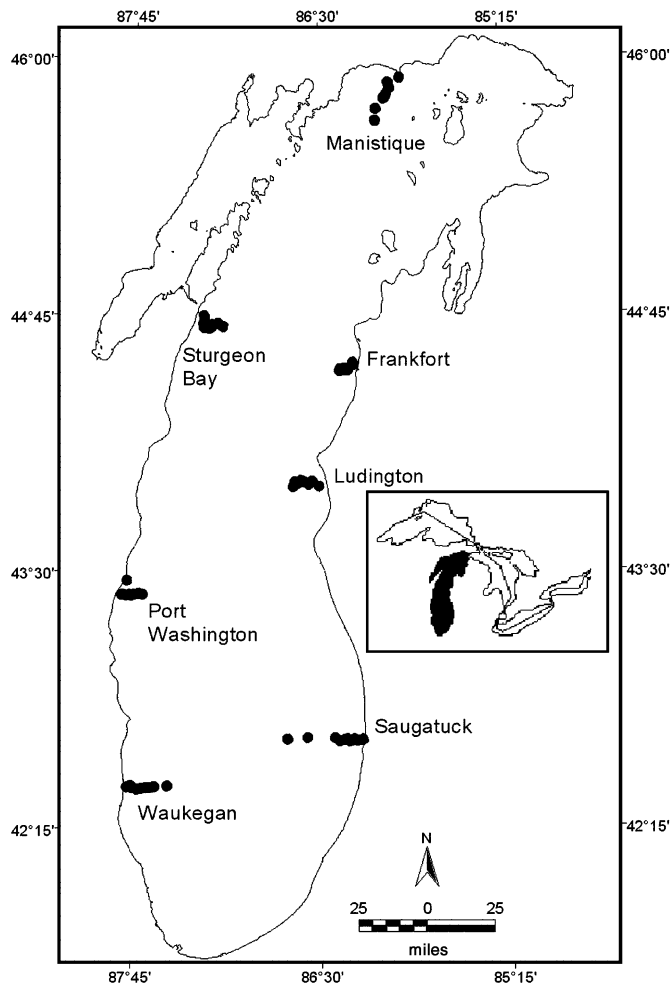
Bloater scales were collected annually for age determinations since 1965 (except for 1966 and 1998). Bloater scale sampling was limited to fish collected at four designated locations (Frankfort, Mich., Saugatuck, Mich., Waukegan, Ill., and Manistique, Mich.) rather than at all locations (except in 1999 when scales were also sampled from Ludington, Mich., and Port Washington, Wis.). From 1965 to 1982, scales were sampled from fish selected at random from the entire bloater size distribution at each of the designated locations. However, since 1983, scale samples have been collected following a stratified sampling design. Scales were collected from a maximum fixed number of fish for each 10-mm length class for each location sampled. The number of scale samples per length class sampled was not constant since 1983, but in most years, about 40 fish were sampled for scales from the most abundant length classes. As would be expected, in some years, very few individuals were sampled from both the smaller and larger length classes. Bloater ages were determined by visual inspection of projected scale images and an age class designation was based on enumeration of observed annuli. Bloater ranged from 0 to 12 years of age. Ageing error was not incorporated in the analysis of size-at-age data. Scored ages were assumed to be true ages

for all fish. The amount of ageing error in scale ageing of bloater populations in the Great Lakes has not been investigated and studies of ageing error in other coregonid species have suggested that the amount of ageing error depends on growth rate, with higher error rates in slower-growing populations (Raitaniemi et al. 1998). Few individuals over age 7 were sampled, and scales were not consistently collected from individuals less than 100 mm in length. Thus, our growth modeling used data for ages 1 to 7 only.

Mean length- and weight-at-age

Because scale samples were not collected at all locations for the entire time period (1965–1999), it was not possible to calculate location-specific mean size-at-age. Previous analysis of the fall bottom trawl data has suggested that the mean size-at-age of bloater differs across the lake (Krause 1999). For this reason, bloater age data were pooled into a northern region (Port Washington, Wis., Sturgeon Bay, Wis., Manistique, Mich., Frankfort, Mich., and Ludington, Mich.) and southern region (Saugatuck, Mich., and Waukegan, Ill.) to calculate regional mean lengths- and weights-at-age (Fig. 2). Bloaters were sampled in both regions for all years except 1965 when only the southern region was surveyed. From 1965 to 1982, when age structures were sampled randomly, the mean length- and weight-at-age in each year and region were calculated by taking the mean of the length and weight, respectively, of all

Fig. 2. Fixed shore locations in Lake Michigan for U.S. Geological Survey – Great Lakes Science Center fall bottom trawl survey. (Inset) Map of the Great Lakes with the international boundary between Canada and the United States of America indicated.



aged fish in each region. From 1983 to 1999 when stratified sampling was used, mean length-at-age ($\bar{L}_{a,y,i}$) in each year and region was estimated by

$$(1) \quad \bar{L}_{a,y,i} = \frac{\sum_j p_{a,y,i,j} p_{y,i,j} \bar{l}_{a,y,i,j}}{\sum_j p_{a,y,i,j} p_{y,i,j}}$$

where $p_{y,i,j}$ is the proportion of the bloater in length bin j from the length–frequency sample for year y and region i , $p_{a,y,i,j}$ is the proportion of age a in length bin j from the scale sample for year y and region i , and $\bar{l}_{a,y,i,j}$ is the mean length-at-age a in length bin j for year y in region i (Gavaris and Gavaris 1983). For large catches (e.g., greater than 20 kg), the total size of the catch and the number of bloater in each length bin were estimated from subsamples of the total catch (see Krause (1999) for details). Mean weight-at-age ($\bar{W}_{a,y,i}$) in each region and year was estimated similarly with $\bar{l}_{a,y,i,j}$ replaced by $\bar{w}_{a,y,i,j}$ (mean weight-at-age a in length bin j in year y and region i). Because the bloater population is generally treated as one stock rather than as two distinct stocks, the regional estimates of size-at-age were averaged to obtain

a lakewide estimate of mean size-at-age ($\bar{L}_{a,y}$ and $\bar{W}_{a,y}$, respectively) for the bloater population.

Abundance indices of bloater and alewife

CPUE data from the annual USGS fall trawl survey were analyzed to derive year-specific indices of relative abundance for adult (age 2+) bloater and alewife, along with yearling bloater. The natural log of the CPUE data was fit to a general linear model incorporating effects for year, location, and depth and allowing correlations among observations from the same location within a year (see Krause (1999)). The estimates of the fixed effects for year were used as an index of relative abundance. These relative indices are expressed on the natural logarithmic scale and differ from the natural log of CPUE by an additive constant. We used these indices to explore the relationship between the changes in bloater growth over time and abundance of yearling and adult bloater, along with adult alewife.

Growth model

We applied a growth model that allowed mean length-at-age to change between years. We also modeled the length–weight relationship in a way that allowed weight-at-length to vary over time. In combination, this allowed us to consider how both weight- and length-at-age changed over time. Dynamics in mean length-at-age were modeled by generalizing the incremental von Bertalanffy growth model to incorporate time-varying growth parameters. Thus, predicted mean length-at-age in a given year depended on mean length of the same cohort in the previous year and the growth parameters for the previous growing season. These predicted mean lengths-at-age were compared with the observed lengths-at-age over all years and adjustments in the growth parameters were made, using a numerical search, to provide the best agreement between the observed and predicted mean lengths-at-age. We were also interested in how the relationship between mean weight-at-age and mean length-at-age changed over time and thus modeled mean weight as a power function of mean length with parameters that were allowed to vary over time. The parameters determining this time-varying relationship were estimated by using them to predict mean weight-at-age using observed mean length-at-age and comparing these predictions to the observed mean weight-at-age. The parameters of the final model are described in Table 1. The dynamic equations used to predict mean length- and weight-at-age and changes in the growth parameters over time are described in Table 2. The equations presented in these tables are referenced by Tx.y, where x is the table number and y is the equation number within Table x .

Length-at-age model

In 1965, mean length-at-age for all ages was predicted by the standard form of the von Bertalanffy growth model (eq. T2.1). For all other years, mean length-at-age for ages 2 and older was predicted by the incremental form of the von Bertalanffy model (eq. T2.2). If the incremental form predicted a negative growth increment, then the growth increment was set to zero. This situation never occurred once the parameter values had converged to the best estimates. Because changes in yearling length over time could not be de-

scribed well by the above model, we modeled yearling length separately as a random walk on the log scale (eq. T2.3). The random walk was started in 1965 at the yearling length predicted by eq. T2.1. This approach allows yearling length to change over time but assumes that yearling length in a given year would tend to be similar to the value from the previous year.

Similarly, we modeled L_∞ as a random walk on the log scale, where ϵ_y is a random change estimated by the model in every year and the random walk was started at L_∞ in 1965 (eq. T2.5). The parameters L_∞ and k were not allowed to vary freely from one another, rather k was assumed to be a linear function of L_∞ with a year-specific random (white noise) deviation (eq. T2.6). This relationship would allow L_∞ and k to have either a positive or negative relationship. The parameters of this relationship and each year-specific random deviation were estimated during the fitting process.

Weight-at-age model

Mean weight-at-age in every year was predicted from observed mean length-at-age ($\bar{L}_{a,y}$) using a length-weight relationship with time-varying parameters (eq. T2.4). Both α_y and β_y were assumed to follow a random walk on the log scale with the starting values in 1965 estimated as parameters during model fitting (eqs. T2.7 and T2.8, respectively).

Model optimization

The model was fitted using AD Model Builder software (Otter Research 2000). AD Model Builder is a superset of C++ that uses automatic differentiation in the application of a quasi-Newton method to fitting nonlinear models, based on a user-specified likelihood equation. In the fitting of this model, the negative log-likelihood function was minimized to obtain parameter estimates. The log-likelihood consisted of seven components:

$$(2) \quad \ell = \ell_1 + \ell_2 + \ell_3 + \ell_4 + \ell_5 + \ell_6 + \ell_7$$

which correspond to those for the observed mean length- and weight-at-age, the random walks, and the white-noise deviations (Table 3). Mean length- and weight-at-age were both assumed to follow a lognormal distribution (eqs. T3.1 and T3.7). The random deviations from the random walks and from the relationship between L_∞ and k were assumed to follow normal distributions (eqs. T3.2–T3.6). Because the variance terms for ℓ_1 – ℓ_7 were either estimated directly during model fitting or provided before fitting, the likelihood components are self-weighting and no additional weighting factors were used.

The variance term, $\sigma_{a,y}^2$, for ℓ_1 (eq. T3.1) was age- and year-specific and composed of two variance components, “measurement error”, σ_m^2 , and “process error”, σ_p^2 . The measurement error parameter captures the changes in the reliability of the mean lengths-at-age as sample size changes. The process error parameter captures any errors that are independent of sample size (e.g., the spatial distribution of certain sizes of bloater in the lake differing between years). The measurement error (on the log scale) was not fitted during the minimization process, rather an estimate was obtained based on the variation in observed lengths-at-age ($\sigma_m^2 = 0.0041$) and treated as a constant.

For ℓ_4 (eq. T3.4), the variance term, σ_k^2 , could not be estimated during model fitting at the same time as σ_∞^2 . Both of these variances refer to process errors for unobserved state variables, and hence there is a singularity in the likelihood surface when their ratio approaches zero or infinity (Schnute and Richards 1995). As an alternative, we modified a strategy used by Schnute and Richards (1995). First we assumed that σ_k^2 was proportional to σ_∞^2 with the proportionality constant, ρ , that was fixed before model fitting. During model fitting, σ_∞^2 was estimated as a parameter and the appropriate value of σ_k^2 was calculated using the estimate of σ_∞^2 and the fixed value of ρ . To choose a value for ρ , we used an iterative approach. First, we fit the model using a wide range of values for ρ to obtain estimates of σ_∞^2 and σ_k^2 . We also calculated the “observed” variances based on the variation in our estimates of ϵ_y and e_y for each value of ρ . By comparing the observed variances in the random deviations to the estimates of the variance components, we found there was only one value of ρ for which these quantities were approximately equal and used this value of ρ in our final model. At this value of ρ , the likelihood profile with respect to ρ is nearly flat. The resulting variances appeared reasonable to us and the resulting model predictions of mean length-at-age were not very sensitive to specific choices for ρ . Although our approach is a repeatable method for obtaining the ratio of these variances, it is an ad hoc approach. Methods for weighting likelihood components when process errors are involved is clearly an area for further research.

The variance components, σ_α^2 and σ_β^2 for ℓ_5 and ℓ_6 (eqs. T3.5 and T3.6, respectively), also could not both be estimated during the fitting process. Instead, as described for variance components of ℓ_4 , we allowed σ_α^2 to be estimated during the model fitting process and then assumed that σ_β^2 was proportional to σ_α^2 with a proportionality constant of ϕ that was fixed during model fitting. The value of ϕ was chosen using the same procedure described for ℓ_4 .

The parameters L_∞ , α , and β in the first year, the intercept of the linear relationship between L_∞ and k , and the variance components must be positive and were restricted to the positive real numbers during model fitting by estimating them on the log scale. All other parameters were estimated on the arithmetic scale.

Other model variants explored

The process of choosing the model structure presented above was based on exploring many variants of a standard von Bertalanffy growth model to find a model structure that adequately described the patterns found in the observed length- and weight-at-age data. We attempted to find the most parsimonious model that provided good predictions of mean size-at-age over time. We assessed model fit by visually inspecting residual plots and by using Akaike’s information criterion (AIC) to compare different models. In this section we will describe several of the different model structures that we investigated to help guide model choice.

In an initial attempt to model the changes in length-at-age, we allowed only L_∞ to be different in each year, keeping k constant over the entire time period, which produced strong patterns in the residuals that we deemed unacceptable. Subsequently, we allowed both k and L_∞ to vary with time independently of one another, but this model failed to converge

Table 1. Parameters and fixed constants for the time-varying von Bertalanffy growth model and weight–length relationship.

Parameter	Description
$L_{\infty 1965}$	L_{∞} for mean length-at-age in 1965
ϵ_y	Random walk deviations for L_{∞}
t_0	Age at length 0 in 1965
b	Intercept of linear function between k and L_{∞}
m	Slope of linear function between k and L_{∞}
e_y	Year-specific deviations for linear function between k and L_{∞}
ξ_y	Random walk deviations for $L_{1,y}$
σ_m^2	“Measurement” error in length-at-age data*
σ_p^2	“Process” error in length-at-age data
σ_{∞}^2	Variance component for L_{∞} random walk
σ_1^2	Variance component for $L_{1,y}$ random walk
ρ	Proportionality constant for variance component for e_y^a
α_{1965}	α from the weight–length relationship in 1965
β_{1965}	β from the weight–length relationship in 1965
v_y	Random walk deviations for α
δ_y	Random walk deviations for β
σ_w^2	Variance component for weight-at-age data
σ_{α}^2	Variance component for the α random walk
φ	Proportionality constant for the variance component of the β random walk ^a
n	Number of years
$n_{a,y}$	Sample size of fish aged in each age and year

*Parameter fixed during model-fitting process. See text for further explanation.

Table 2. Dynamic equations used to predict mean length- and weight-at-age and changes in growth parameters over time.

Mean length- and weight-at-age	
T2.1	$L_{a,1965} = L_{\infty 1965} (1 - e^{-k_{1965}(a-t_0)})$
T2.2	$L_{a+1,y+1} = L_{a,y} + (L_{\infty y} - L_{a,y})(1 - e^{-k_y})$
T2.3	$\log(L_{1,y+1}) = \log(L_{1,y}) + \xi_y$
T2.4	$\hat{W}_{a,y} = \alpha_y \bar{L}_{a,y}^{\beta_y}$
Growth parameters	
T2.5	$\log(L_{\infty y+1}) = \log(L_{\infty y}) + \epsilon_y$
T2.6	$k_y = b + mL_{\infty y} + e_y$
T2.7	$\log(\alpha_{y+1}) = \log(\alpha_y) + v_y$
T2.8	$\log(\beta_{y+1}) = \log(\beta_y) + \delta_y$

Note: $L_{a,y}$ is the predicted mean length-at-age a in year y ; $\bar{L}_{a,y}$ is the observed mean length-at-age a in year y ; $\hat{W}_{a,y}$ is the predicted mean weight at observed mean length-at-age a in year y ; $L_{\infty y}$ is the asymptotic length in year y ; k_y is the Brody growth coefficient in year y ; and α_y and β_y are the parameters of the weight–length relationship in year y .

on a solution. In an attempt to allow both L_{∞} and k to vary over time but in a correlated manner, we attempted to incorporate the functional relationships between L_{∞} and k (of the general form $k = qL_{\infty}^g$) proposed by Jensen (1996), but none of these models would converge on a solution, apparently because the assumed negative relationship does not agree with the observed data. We then fitted a model where k was

a linear function L_{∞} , which was able to converge on a solution but still had strong patterns in the residuals, particularly for yearlings (age 1). To remove these patterns in the residuals, we arrived at the model presented above. We also attempted to capture the change in mean weight-at-age by allowing only α or β to vary with time, but we found that the AIC for the model in which both α and β were allowed to vary with time was lower than either of these simpler models.

Finally, we also fit a cohort-based model (i.e., growth parameters differed between cohorts but remained constant across a given cohort's life) because the growth patterns appeared to be correlated across years. However, we found that this model structure produced very strong patterns in the residuals and was unable to capture the changes in growth that occurred in the late 1990s. For this reason, we deemed this type of model unacceptable.

Results

Model fit

Although the measurement error variance (σ_m^2) was 6.81 times larger than the process error (σ_p^2 ; Table 4), the contribution of measurement error to total variance in predicted mean length-at-age declines rapidly with increasing sample size. For example, for a sample size of 10, the measurement error contributes ~40% to the total variance in predicted mean length-at-age, but its contribution declines to ~21% for a sample size of 25. Across all years and ages, 28% of the observed sample sizes (65 of 234 age–year samples) were

Table 3. Log-likelihood components (ignoring constants) for bloater growth model.

T3.1	ℓ_1 : mean length-at-age	$\sum_y \sum_a -0.5 \left(\log(\sigma_{a,y}^2) + \frac{(\log(L_{a,y}) - \log(\bar{L}_{a,y}))^2}{\sigma_{a,y}^2} \right)$ $\sigma_{a,y}^2 = \sigma_p^2 + \sigma_m^2 / n_{a,y}$
T3.2	ℓ_2 : random walk in L_∞	$-\frac{n-1}{2} \log(\sigma_\infty^2) - \frac{0.5}{\sigma_\infty^2} \sum_y \varepsilon_y^2$
T3.3	ℓ_3 : random walk in $L_{1,y}$	$-\frac{n-1}{2} \log(\sigma_1^2) - \frac{0.5}{\sigma_1^2} \sum_y \xi_y^2$
T3.4	ℓ_4 : year-specific deviations in k	$-\frac{n}{2} \log(\sigma_k^2) - \frac{0.5}{\sigma_k^2} \sum_y e_y^2$
T3.5	ℓ_5 : random walk in α	$-\frac{n-1}{2} \log(\sigma_\alpha^2) - \frac{0.5}{\sigma_\alpha^2} \sum_y v_y^2$
T3.6	ℓ_6 : random walk in β	$-\frac{n-1}{2} \log(\sigma_\beta^2) - \frac{0.5}{\sigma_\beta^2} \sum_y \delta_y^2$
T3.7	ℓ_7 : mean weight at mean length	$\sum_y \sum_a -0.5 \left(\log \left(\frac{\sigma_w^2}{n_{a,y}} \right) + \frac{(\log(\hat{W}_{a,y}) - \log(\bar{W}_{a,y}))^2}{\frac{\sigma_w^2}{n_{a,y}}} \right)$

Note: Parameters are defined in the text and Table 1.

less than 25. There was a higher percentage of sample sizes less than 25 in the yearling (33.3%) and older ages (age 5, 24%; age 6, 45%; age 7, 72%) than in the intermediate ages (age 2, 15%; age 3, 6%; and age 4, 3%). The model fit indicates a positive correlation between L_∞ and k (Table 3), implying that in years when L_∞ was high, k is also high (Fig. 3c). This result is contrary to many theoretical and empirical studies, which describe an inverse relation between L_∞ and k (Pauly 1980; Jensen 1996).

The residuals for both mean length-at-age and mean weight-at-age from this model were generally moderate in size, with most within ± 2 standard deviations (SD), and only in three cases was the value outside the range ± 3 SD. Moreover, the residuals generally exhibited no pattern with year at each age. We examined those specific cases in which there appeared to be a potential temporal pattern in the residuals. The first case was mean length-at-age 4, where there appeared to be a slight trend of negative residuals in the earlier years changing towards positive residuals in the later years. Because these residuals were relatively small in magnitude, they may simply represent a minor departure from the assumed von Bertalanffy growth model. We did not deem this minor departure of sufficient magnitude to explore a more flexible growth model such as the model proposed by Schnute (1981). The second and third cases, mean weight-at-ages 1 and 7, showed opposite trends. In predicting mean weight-at-age 1, the model slightly overestimated mean weight in the earlier years and underestimated it for later years in the series. For mean weight-at-age 7, the model tended to underestimate mean weight in the earlier years and overestimate it in later years. We interpret these results to indicate that our model may not have captured all of the com-

Table 4. Parameter estimates and asymptotic standard errors (in parentheses) ($p = 18.16$ and $\phi = 2.75 \times 10^{-3}$).

Parameter	$\sigma_m^2 = 0.0041$
t_0	-3.641 (0.477)
b	2.164×10^{-22} (7.65×10^{-17})
m	5.98×10^{-4} (7.68×10^{-5})
σ_p^2	7.40×10^{-4} (1.20×10^{-4})
σ_∞^2	4.51×10^{-5} (1.21×10^{-5})
σ_1^2	2.56×10^{-4} (1.03×10^{-4})
σ_w^2	0.199 (2.66×10^{-2})
σ_α^2	8.76×10^{-5} (3.18×10^{-5})

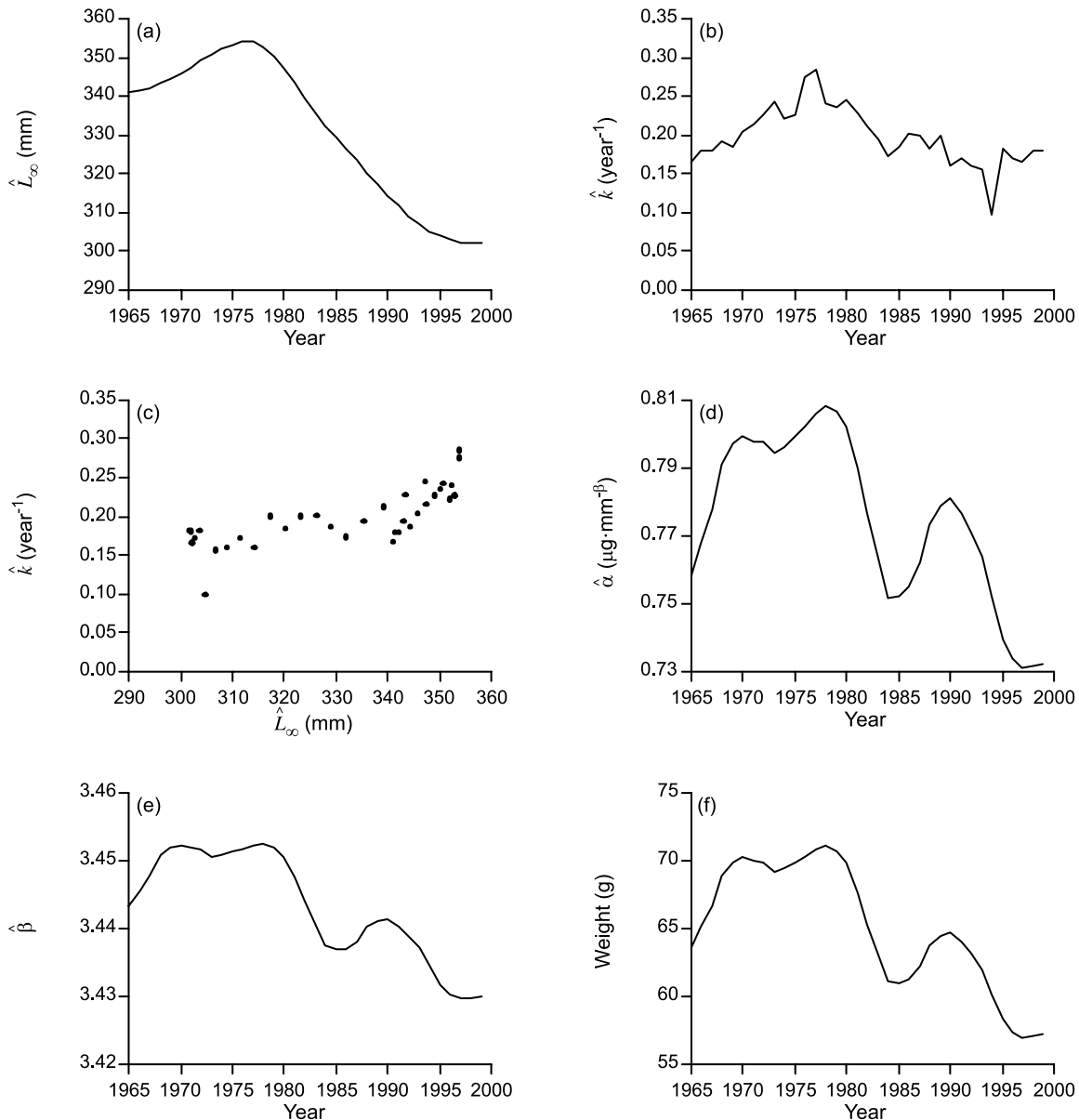
Note: This table contains all of the parameters that do not vary with time.

plexities in changes in the bloater length–weight relationship over time and that the factors that influenced the weight at mean length of younger and older bloaters may be different.

Bloater growth dynamics

The trends in estimates of both L_∞ and yearling length show a substantial decline over the latter portion of the study period (Figs. 1b, 3a). Estimates of L_∞ peaked in 1976–1977 at a value of 354 mm, then declined steadily through the 1980s and 1990s to 302 mm by 1999 (Fig. 3a). Yearling length declined from a maximum of 183 mm in 1965 to 135 mm in 1987 but subsequently has increased slightly (Fig. 1b). The estimates of k show a similar decline in the 1980s (Fig. 3b). Predicted and observed mean length-at-ages 2–7 showed an increasing mean length through the 1970s

Fig. 3. Estimates of (a) L_{∞} , (b) k , (d) α , (e) β , and (f) predicted mean weight of a 200-mm bloater (*Coregonus hoyi*) over time. (c) The estimated relationship between k and L_{∞} in the Lake Michigan bloater population.



and then declined sharply through the 1980s (Figs. 1b–1d). In recent years, mean length for all ages appears to be increasing slightly.

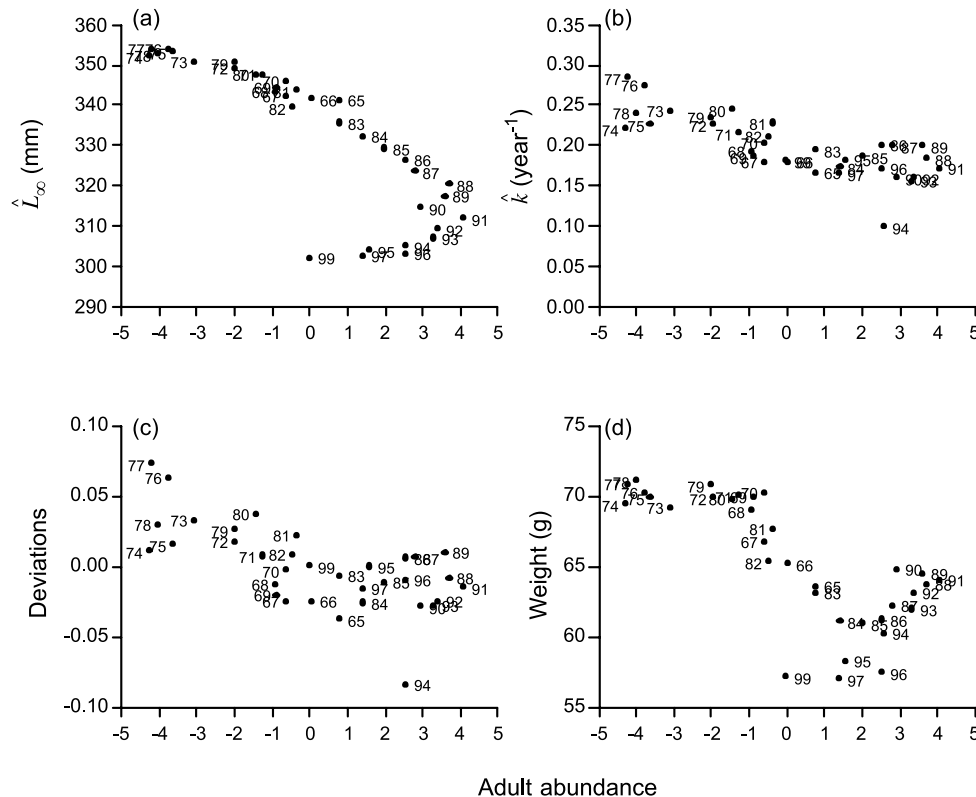
Estimates of α and β from the length–weight relationship show similar patterns of change over time (Figs. 3d, 3e). Both increased during the late 1960s and remained relatively high throughout the 1970s. During the 1980s they declined initially and then increased during the late 1980s before declining again in the 1990s. The predicted weight of an intermediate-sized bloater (200 mm) over time increased through the early 1980s and subsequently declined after a slight recovery in the early 1990s (Fig. 3f).

To assess the role that density-dependent mechanisms may play in regulating bloater growth, we graphically explored the relationships between the estimates of growth parameters and bloater population abundance. Estimates of L_{∞} and the relative abundance of adult (age 2+) bloater appears to be in-

versely related during most of the study period (Fig. 4a). However, as adult bloater abundance peaked and then declined during the 1990s, estimates of L_{∞} did not respond in an anticipated density-dependent fashion. In contrast, k shows a more regular linear decline with increased adult abundance (Fig. 4b). There appears to be a slight change in this trend at high relative adult abundance. If we factor out the effects of changes in L_{∞} by only looking at the estimated random deviations (e_y), this feature is more apparent (Fig. 4c).

The temporal pattern in the bloater length–weight relationship through the mid-1980s also suggests density-dependent effects. Our estimates of the mean weight at 200 mm from 1965–1984 appear to follow a similar pattern with higher weight during periods of lower bloater abundance (Fig. 4d). However, during the late 1980s and early 1990s, mean weight increased despite the higher adult bloater abundances. This transient temporal response of mean weight at 200 mm was

Fig. 4. Relationship between estimates of (a) L_{∞} , (b) k , and (c) deviations (e_t) from the linear relationship between L_{∞} and k and (d) predicted mean weight of a 200-mm bloater (*Coregonus hoyi*) and the relative abundance of adult (age 2+) bloater in Lake Michigan, 1965–1999.



not seen in the von Bertalanffy parameters. Subsequently, mean weight at 200 mm returned to low levels and, like L_{∞} , did not increase in the late 1990s despite lower bloater abundance.

Density-dependent growth also appears to occur for yearling bloaters. The relationship between estimated yearling length and yearling relative abundance shows decreased yearling size with increased abundance of yearlings (Fig. 5a). However, in the most recent years (1994–1999), as was seen for the adult growth parameters, this relationship appears to have broken down. Juvenile bloater growth and adult alewife abundance are positively correlated from 1965 to 1999, with larger yearling length achieved in times of high alewife abundance (Fig. 5b).

Discussion

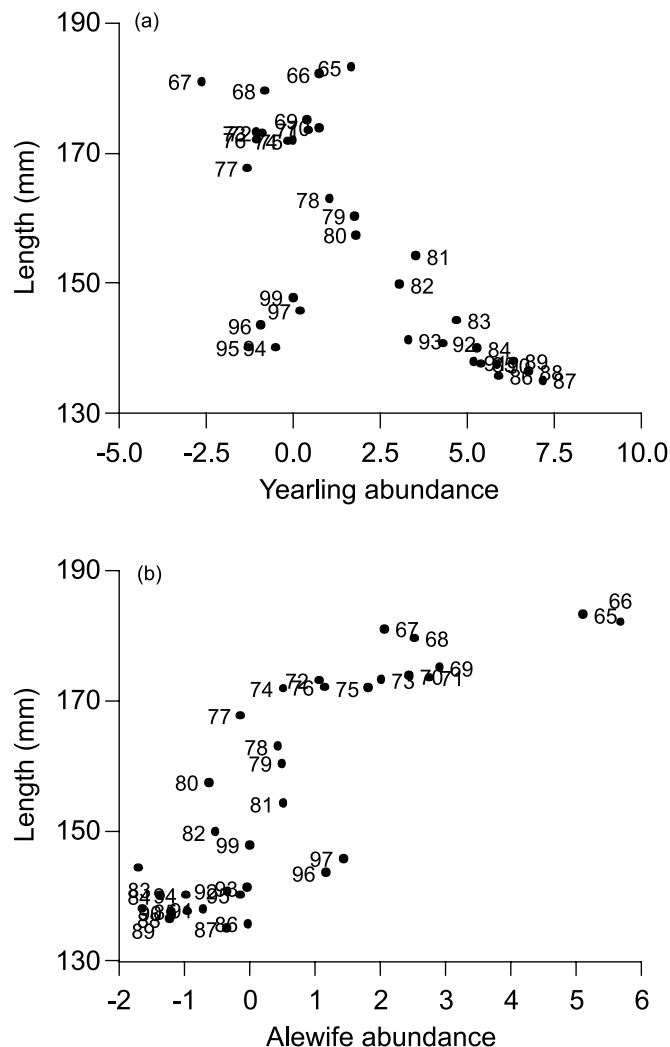
We were able to capture the dramatic changes in bloater size-at-age by modeling changes in L_{∞} , k , α , β , and yearling length. The model, in general, predicted mean length- and weight-at-age that agreed very well with observed data. Some patterns were detected in the residuals, but these patterns appear to be only minor deviations from our growth model. Although limits with regard to estimability were encountered (e.g., we could not estimate k independently for each year), we were still able to capture the dynamics and infer the mechanisms of the changes in bloater growth over time.

Our model shares features with some previous attempts to fit dynamic growth models to mean length-at-age data (Millar and Myers 1990; Millar et al. 1999). Unique features of our

approach included using a time series approach to describe changes in growth parameters over time (i.e., random walks) rather than assuming relationships with environmental factors and combining length- and weight-at-age information in the description of changes in growth over time. By using a dynamic growth model, such as the model presented here, the noise inherent in mean size-at-age data can be smoothed, eliminating the negative growth increments that are often observed when calculated directly from observed size-at-age. Furthermore, the parameters of the growth model provide a useful and parsimonious way of summarizing how growth is changing over time and allow researchers to investigate mechanisms for changes in growth over time using information from all ages rather than a selected few.

The incremental growth model presented here allowed all fish of the same size, regardless of their previous growth history, to achieve the same growth. This feature allowed for fish to recoup size-at-age even after previous poor growth if conditions improved. As such, this model would not be able to emulate stunting (the phenomenon of previous growth history influencing current growth potential; Ylikarjula et al. 1999). Although we did not see evidence for stunting in the Lake Michigan bloater population, our ability to detect this condition may be obscured because of the relatively slow change in conditions over time and the observation that most individuals experiencing poor growth conditions in early life also experience poor growth conditions as an adult. If further evidence suggests that stunting may be important in bloater growth dynamics, then the dynamic growth model would need to be adjusted to incorporate this process. Millar and

Fig. 5. Relationship between estimated yearling length and (a) relative abundance of yearling bloater (*Coregonus hoyi*) in Lake Michigan, 1965–1999, and (b) relative abundance of adult (age 2+) alewife (*Alosa pseudoharengus*) in Lake Michigan, 1965–1999.



Myers (1990) have explored one model that incorporates stunting and could be used in an analysis similar to ours.

Our analysis indicates a positive relationship between L_{∞} and k in the Lake Michigan bloater population. Previous studies of fish growth have shown that the relationship between L_{∞} and k is generally negative (Pauly 1980; Jensen 1996). However, Pauly (1980) looked at this relationship across populations, whereas we looked within one individual fish population. We have tried several functional forms to force a negative relationship between L_{∞} and k ; however, none of these models was able to converge on a solution. The positive relationship that we observed, although initially counterintuitive, simply implies that when growth conditions are favorable for bloaters, they respond with both fast growth rates and larger maximum sizes.

Our analysis corroborates a previously reported density-dependent growth response of bloater in Lake Michigan (TeWinkel et al. 2002). All of the growth parameters esti-

mated seemed to decline in concert with increasing bloater abundance. However, since the beginning of the 1990s, a change in this relationship appears to have occurred. During this time, bloater growth in length and mean weight at 200 mm remained low despite relatively low abundances of both adult and juvenile bloater. We note that these recent changes in bloater growth were coincident with the invasion and expansion of zebra mussels (*Dreissena polymorpha*) and the disappearance of *Diporeia* spp. in Lake Michigan (Nalepa et al. 2000; Fleischer et al. 2001). *Diporeia* represents a major link between pelagic production and upper trophic levels in Lake Michigan and is also an important component of adult bloater diet in Lake Michigan, exhibiting higher lipid content than other benthic macroinvertebrates (Gardner et al. 1985; Rand et al. 1995; Davis et al. 1997). Zebra mussels may also be having profound effects on the primary productivity of Lake Michigan because of energetic demands (Madenjian 1995; Stoekmann and Garton 1997) that may manifest in lower productivity in lower trophic level fishes.

Interestingly, the changes in bloater growth in the 1990s are evident in the estimates of L_{∞} and yearling length but not in the estimates of k . This suggests that although all three growth parameters may be affected by intraspecific density, changes in the food web can influence them differently. Such a difference could arise if the change in the food web caused approximately the same effect on incremental growth (in length), irrespective of fish size (see Walters and Post 1993). Only future monitoring of bloater length-at-age will tell if these trends continue in the future and if these changes in bloater growth are a harbinger of future changes to the Lake Michigan ecosystem.

Our inability to model changes in growth of both adult and juvenile bloater with a common set of parameters suggests that these life stages of bloater may be responding to different environmental conditions. This result is not unexpected because of the different bathymetric habitats occupied by the two life stages. Juvenile bloater occupy more nearshore, shallower depths and feed primarily on zooplankton, whereas adult bloater are limited to a hypolimnetic distribution and feed primarily on hypolimnetic prey (Davis et al. 1997). Consequently, intraspecific density-dependent growth in bloaters appears to be life stage specific (i.e., juvenile growth appears to respond strongly to juvenile abundance but not to adult abundance, and adult growth seems to respond primarily to adult abundance).

Previous studies have concluded that the invasion of the exotic alewife (*Alosa pseudoharengus*) has had profound effects on the bloater population in Lake Michigan (e.g., Crowder and Crawford 1984; Eck and Wells 1987). For example, Crowder and Crawford (1984) suggested that competition between the pelagic juvenile bloater and adult alewife for pelagic resources has caused bloater to switch to benthic resources at an earlier age (from age 3 to age 2). If competition between juvenile bloater and adult alewife was strong, we would expect that in times of high alewife abundance, juvenile bloater growth would be reduced. In fact, young bloater growth rate, as indicated by predicted yearling length, increased in concert with adult alewife abundance. This suggests that any negative interaction between juvenile bloater and adult alewife does not appear to affect juvenile

bloater length, at least within the densities of alewife and bloater observed during the study period (1965–1999).

The implications of density-dependent growth in bloater for the Lake Michigan ecosystem may be profound. Since the mid-1980s, concern about the balance between the predatory demands of stocked salmonids and the productivity of the forage base has risen. Several observations indicate that the forage available to the salmonids, particularly the chinook salmon (*Oncorhynchus tshawytscha*), may not be sufficient to maintain the large populations of the 1980s (Stewart and Ibarra 1991; Holey et al. 1995). Bloater, especially smaller individuals, represent a potentially important alternative forage item for the salmonids (Madenjian et al. 1998). Therefore, in the future, an understanding of the forces governing bloater dynamics will be important in balancing predatory demand and forage availability. Changes in size-at-age may have many effects on their population dynamics, including mortality rates and fecundity. Our ability to accurately assess the availability of forage for salmonids depends in part on our understanding of bloater population dynamics.

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